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Quantifying the relative contribution of *ante*- and *post-mortem* factors to the variability in beef texture

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This study aims to investigate the relative contribution of ante- *and* post-mortem *factors to the final quality of beef. In all, 112 steers (four breed-crosses) were arranged in a 2 × 2 × 2 factorial experimental including production system, growth implant and β-adrenergic agonist strategies. Carcasses were suspended by the Achilles tendon or the aitch bone and meat was aged for 2/6/13/21/27 days (*longissimus *muscle) or 2/27 days (*semimembranosus *muscle). Meat quality traits related to beef texture were measured. Statistical analyses were developed including* ante- *and* post-mortem *factors and their relative contribution to the variability observed for each measured trait was calculated. The main factor responsible for the variability in sarcomere length was the suspension method (91.1%), which also influenced drip-loss (44.3%). Increasing the percentage of British breeds increased (*$P < 0.05$*) the intramuscular fat content in* longissimus *muscle, but only when implants were not used. Thus, the breed-cross, implant strategy and their interaction were responsible for >58% of the variability in this trait. The variability in instrumental and sensory tenderness was mainly affected by* post-mortem *factors (carcass suspension, ageing time and their interaction), explaining generally ~ 70% of the variability in these traits. Breed-cross was the second most important effect (~15%) when carcass suspension was not considered in the model, but still ageing time was responsible for a much larger proportion of the variability in tenderness (>45%). In conclusion,* post-mortem *handling of the carcasses may be much more effective in controlling beef tenderness than* pre-mortem *strategies.*

Keywords: ageing, β-agonist, carcass suspension, finishing, implant

Implications

Under the conditions simulated in this study, including breed-cross, production system, use of implants and/or β-agonists, carcass suspension and ageing time in a single study has been able to explain more than 70% of the variability in beef tenderness. Therefore, a large amount of the inconsistency in beef tenderness at the consumer level could be controlled by manipulating these factors. Moreover, the large amount of variability already explained and the possibility of quantifying the impact of each factor on the final tenderness opens the door to a new way of approaching beef quality manipulation. Besides the potential use of this information for breeding programs or development of new production systems, understanding the effect and interactions of the different factors present in the production chain is the first step in developing palatability assurance critical control point systems.

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Introduction

Tenderness is one of the most important quality attributes in beef (Jayasooriya *et al.*, 2007). Consistency in beef tenderness at the consumer level has been one of the main challenges in meat quality research for at least five decades (Koohmaraie, 1994). However, recent reports still consider it a current and long-term goal for beef producers (Flowers, 2011). The relative lack of success to date in controlling tenderness is due to the complex interactions influencing this trait. In this context, grading systems such as Meat Standards Australia beef-grading scheme (Polkinghorne *et al.*, 2008) have included several production and processing factors in order to provide a guaranteed satisfaction to

the consumer by reducing the potential variability in beef tenderness.

Numerous factors, either *ante-mortem*, such as genotype, production system, age or live weight, growth promotants, or *post-mortem*, such as carcass suspension or ageing time, have been shown to affect tenderness (Ferguson *et al*., 2001). Meat texture of different beef breeds and genotypes has been reported to vary in numerous studies (Mandell *et al*., 1997; Dikeman *et al*., 2005; Christensen *et al*., 2011). Alternative beef production systems, including reducing age at slaughter, may result in younger, higher marbled beef, but with lower carcass weights and smaller steak portion size (Schoonmaker *et al*., 2002). However, the effects on meat tenderness have been inconsistent (Klopfenstein *et al*., 2000; Schoonmaker *et al*., 2002; Meyer *et al*., 2005). Anabolic implants are used in the beef industry to improve growth rates and feed efficiency during finishing. However, the side effects of using implants may include reduced marbling scores, increased incidence of dark cutting and decreased tenderness (Foutz *et al*., 1997; Roeber *et al*., 2000; Reiling and Johnson, 2003). Regarding *post-mortem* factors, alternative carcass suspension methods such as aitch bone suspension, pelvic suspension or Tenderstretch have been reported to improve beef tenderness compared with traditional Achilles tendon suspension (Aalhus *et al*., 1999). Finally, ageing of beef is universally thought to improve tenderness (Johnston *et al*., 2001) as a result of the proteolysis of myofibrillar proteins (Koohmaraie, 1996).

Knowledge of the quantitative significance of each factor is important to assess their economic value, as well as to choose the correct selection traits to improve the profitability and quality of animal products and to develop efficient integrated management strategies (Juárez *et al*., 2008). The approach used in this study evaluates the relative importance of the several (cross-breed, production system, implant, β-agonist, suspension, ageing time) factors and their interactions to quantify their relative contribution to variation in beef texture.

Material and methods

Animal management

In order to evaluate the relative contribution *of ante-mortem* factors, 112 steers from four breed-crosses: >75% Continental, 50% to 75% Continental, 50% to 75% British and >75% British were arranged in a $2 \times 2 \times 2$ factorial experimental at the Agriculture and Agri-Food Canada Lacombe Research Centre (Lacombe, Alberta, Canada). The experimental design included production system (12 to 13 months, calf-fed *v.* 18 to 20 months, yearling-fed), implant (not implanted *v.* implanted with 200 mg progesterone and 20 mg estradiol benzoate at weaning followed by 120 mg of trenbolone acetate and 24 mg estradiol 83 days after first implantation and every 80 to 90 days before receiving their last implant of trenbolone acetate/estradiol) and β-adrenergic agonist (no ractopamine *v.* 200 mg ractopamine per head per day for 28 days). Steer calves were allocated to production systems and implant groups based on breed-cross, birth date and calf weight. The production systems were described in detail by Basarab *et al*. (2007 and 2011). Briefly, calf-fed steers were placed into a feedlot pen fitted with eight GrowSafe® feeding stations (GrowSafe® System Inc., Airdrie, Alberta, Canada) where they were fed twice daily *ad libitum* and adjusted from a high forage-based diet to a high grain finishing diet over 27 to 42 days. The adjustment period was followed by an 80 to 86 days test period where the steers were fed twice daily *ad libitum* a finishing diet. The average ingredient composition of the diet (as fed basis) fed during the finishing phase was 57.5% rolled barley grain, 35.0% barley silage and 7.5% protein supplement and premix. Yearling-fed steers, following weaning, were placed on meadow-brome grass (*Bromus riparius* Rehm.) alfalfa (*Medicago sativa* L.) pasture where they rotationally grazed for 52 days. Then, a backgrounding diet consisting of 64.0% barley silage, 26.1% hay and 9.9% grain was fed for 192 days. After the backgrounding period, the steers grazed meadow-brome alfalfa pastures for 90 days. Yearling-fed steers were then placed into a feedlot pen fitted with eight GrowSafe® feeding stations where they were fed twice daily *ad libitum* and adjusted from a high forage-based diet to a high grain finishing diet over 21 to 23 days. The 3-week adjustment period was followed by an 86 days test period where the steers were fed twice daily *ad libitum* a finishing diet. The average ingredient composition of the diet (as fed basis) fed during the finishing phase was 60.46% rolled barley grain, 35.18% barley silage and 4.36% protein supplement and premix. All dietary treatments and experimental procedures were approved by the Lacombe Research Centre Animal Care Committee and animals were cared for in accordance with guidelines established by the Canadian Council on Animal Care (CCAC, 1993).

Carcass handling and sampling

Steers were targeted for slaughtered at a constant backfat thickness of 8 to 9 mm as determined by ultrasound taken 1 to 2 months before harvest. Steers were stunned, exsanguinated and dressed in a simulated commercial manner at the federally inspected abattoir of the Lacombe Research Centre. For all the animals, alternate sides of the carcass were used such that the left side served as the control (traditional Achilles' tendon carcass suspension) and the right side as the altered suspension (aitch bone or pelvic bone suspension). The carcasses were then chilled at 2°C overnight for 24 h. At 24 h after slaughter, the *longissimus* and *semimembranosus* muscles from both carcass sides were removed and trimmed of subcutaneous fat and overlying muscles for subsequent meat quality analyses.

Each *longissimus* muscle was fabricated into 11 steaks (2.54 cm thickness). The first and second steaks were used for sarcomere length and drip-loss measurements in fresh meat. The next five steaks were aged for 2, 6, 13, 21 or 27 days *post mortem*, in order to analyze instrumental texture in fresh meat. The eighth and ninth steaks were aged for 2 or 27 days and frozen for subsequent sensory analysis. Finally, the last two steaks were also aged for 2 or 27 days and used to determine proximate composition in fresh meat. The *semimembranosus* muscle was fabricated into three

pairs of steaks (six in total), which were aged for 2 or 27 days and used for instrumental texture, sensory analysis and proximate composition determination. All samples were labeled, individually vacuum packaged (Ultravac Model UV2100; Koch Instruments, Kansas City, MO, USA) and placed in a cooler at 2°C. Steak locations within each muscle and type of analysis were rotated to ensure equal representation of muscle location within each ageing time.

Meat quality analyses

Sarcomere length was measured as described by Aalhus *et al*. (1999). Briefly, 2 g of muscle freed of fat and connective tissues were removed, scissor-minced and mixed in 20 ml of a 0.02 M ethylene glycol tetraacetic acid/0.25 M sucrose solution in a 50 ml centrifuge tube. Samples were homogenized for 10 s at 6000 r.p.m. using a Polytron Homogenizer PT3100 and a 2 cm generator (Brinkmann Instruments Inc., Mississauga, ON, Canada). One drop of each sample was placed on a slide with a cover slip for observation with an Axioscope (Zeiss, Munich, Germany) equipped with a Sony DXC 930 Color Video Camera (Sony Corporation, Tokyo, Japan). Three sarcomere lengths were measured per image with Image Pro-Plus software V4.0 (Mediacybernetics, Silver Spring, MD, USA) and 10 images were analyzed per muscle sample. Lengths were averaged and expressed in micrometers.

To determine drip-loss, one steak was weighed and placed into a polystyrene tray with a dri-loc pad (UZ Soaker Ultra Zap Pads, Paper Pak Industries, Washington, GA, USA), overwrapped with oxygen permeable film (8000 ml/m^2 per 24 h vitafilm choice wrap; Goodyear Canada Inc., Toronto, ON, Canada) and displayed in retail case at 1°C for 6 days, as described by Nassu *et al*. (2011). A final steak weight was then recorded and drip-loss percentage was calculated.

Following the ageing time, proximate analysis, shear force determinations and sensory evaluations were conducted on both muscles (*longissimus* and *semimembranosus* muscle). The steaks for proximate analysis were trimmed of all subcutaneous fat and finely comminuted (Robot Coupe Blixir BX3; Robot Coupe USA Inc., Ridgeland, MS, USA). Moisture content was then determined as the weight lost during heating 100 g of ground tissue at 102°C for 24 h until constant weight was achieved (VWR Scientific Model 1370FM; Mississauga, ON, Canada). After drying, samples were analyzed for CP (Association of Official Analytical Chemists (AOAC), 1995; Official Method 981.10) and crude intramuscular fat extracted with petroleum ether (AOAC, 1995; Official Method 991.36).

Steaks for shear force determination were kept in a cooler at 2°C until the time of cooking. Before cooking for shear force determinations, spear point temperature probes (10 cm) were inserted into the mid-point of all steaks. They were then placed on a grill (Garland Grill ED30B, Condon Barr Food Equipment Ltd., Edmonton, AB, Canada) preheated to $\sim$ 210°C. Steaks were grilled to an internal temperature of 35°C, turned and cooked to a final temperature of 71°C. Steaks were placed into polyethylene bags, sealed and immediately immersed in an ice/water bath to prevent further cooking. They were then transferred to a 1°C cooler to allow standing for a 24 h period. Six cores, 1.9 cm in diameter, were removed parallel to the fiber grain and peak shear force determined on each core perpendicular to the fiber grain using a TA-XT Plus Texture Analyzer equipped with a Warner–Bratzler shear head at a crosshead speed of 20 cm/min using a 30 kg load cell and Texture Exponent 32 Software (Texture Technologies Corp., Hamilton, MA, USA). Peak shear force was expressed as the average of the six cores (Juárez *et al*., 2011). On each subsequent testing day, trays of steaks were removed from the cooler and shear force determined as described.

Taste panel steaks were removed from the freezer (freezing time 3 to 6 months) and placed in a refrigerator to thaw for 24 h. Samples were blocked by treatment and ageing time. Implant, β-agonist, carcass suspension and biotype were balanced across the sessions (two sets of four samples per session). Steaks were grilled and prepared for sensory analysis as described for shear force determinations. Attribute ratings from panelists (eight members) were electronically collected with Compusense 5, release 4.6 computer software (Compusense Inc., Guelph, ON, Canada) using an 8-point descriptive scale for initial and overall tenderness (8 = extremely tender; 1 = extremely tough) and initial and sustainable juiciness (8 = extremely juicy; 1 = extremely dry). Panelist training was based on published standards and guidelines (American Meat Science Association (AMSA), 1995; ASTM-International, 2009) with panelists previously extensively trained for evaluation of meat.

Statistical analyses

Statistical analyses for all the studied traits were developed using the MIXED model Covtest procedure of SAS (SAS, 2003), including the individual *ante*- (cross-breed, finishing, implant, β-agonist) and *post-mortem* (suspension, ageing time) factors and their interactions as fixed effects. The degree of fatness, nested within implant, β-agonist and finishing, was used as a covariate. The individual animal, nested within implant, β-agonist and finishing, was included as a random factor. The adjusted multiple R^2 (representing the overall fit of the proposed model or the variability of trait explained for the analyzed factors) was calculated for the full model (Edwards *et al*., 2008). Alternative models, removing non-significant interactions, were tested to achieve the highest accuracy. Individual factors were then removed from the model and the decrease in the R^2 value was used to calculate the relative contribution of that given factor on the variability observed for each measured trait. An *F*-statistic test based on the extra sum of squared residuals in a reduced model over a full model was used to assess the significance of the relative contribution of each factor, as described by Juárez *et al*. (2008). Treatment means were determined using the least square means option and separated using an *F*-test protected Latin square design ($P \leqslant 0.05$). The analyses were then repeated in a model excluding the effect of carcass suspension and the data from the carcass sides suspended by the aitch bone in order to evaluate the relative contribution of

the rest of the factors in a system using conventional Achilles' tendon suspension only. Only the significant interactions ($P > 0.05$) or those absorbing >5% of the variability for any trait were presented in the tables.

Results and discussion

Drip-loss and sarcomere length

The effects of the main factors and the significant interactions on drip-loss and sarcomere length in *longissimus* muscle are presented in Table 1. Although production system, β-adrenergic agonist strategy, carcass suspension and their three-way interaction had an effect ($P < 0.05$) on drip-loss value, carcass suspension was the only factor influencing ($P < 0.001$) the length of the sarcomere in *longissimus* muscle. Breed-cross and implant strategy had no effect ($P > 0.05$) on drip-loss and sarcomere length. The effect of the individual animal variation was significant ($P < 0.05$) for both traits. Thus, the variability in sarcomere length explained by the model ($R^2 = 0.76$) was mainly due (91.1%) to differences between suspension methods (Table 2). This factor was also responsible for 44.3% of the variability in drip-loss. Moreover, drip-loss was also highly affected by production system (15.3%) and β-agonist strategy (19.5%). The individual animal variation explained 8.5% of the variability in drip-loss, but <1% in sarcomere length. Lower drip-loss values were observed in meat from yearling-fed steers, without β-adrenergic agonist and in carcass sides suspended by the aitch bone, compared with meat from calf-fed steers, with β-agonists and suspended by the Achilles' tendon (Figure 1). Thus, although these three factors were responsible for >79% of the variability explained by the model ($R^2 = 0.58$), their interactions did not explain >5% of the variability in drip-loss.

Pelvic suspension has been shown to dramatically increase sarcomere length in muscles such as *longissimus lumborum* and *semimembranosus* (Park *et al*., 2008). In this study, carcass sides suspended by the Achilles' tendon also presented much lower sarcomere length values (1.73 ± 0.05 μm) than those suspended by the aitch bone (2.30 ± 0.05 μm). These values are similar to those reported in previous studies (Eikelenboom *et al*., 1998; Sørheim *et al*., 2001; Park *et al*., 2008) confirming the strong influence of pelvic suspension on the length of the sarcomere in *longissimus* muscle, which may have an important effect on beef tenderness and branding programs wishing to assure tenderness of their beef products. According to previous studies that stretching also results in a decrease in drip-loss values in beef (Aalhus *et al*., 2000) due to increased carcass shrink losses, and subsequent reduced purge losses, and it can have an interactive effect with the beef production system and slaughter age (Ahnström *et al*., 2009). Dubeski *et al*. (1997) also found lower drip-loss values in yearling-fed animals, which could be due to different carcass cooling rates. Higher drip-loss values have also been reported for meat from animals with β-agonist treatments (Strydom *et al*., 2009). However, the effects seem to be associated to dose and duration of treatment, as well as type of β-agonist.

Table 1 *Least square means (±s.d.) and factors (P-value) affecting beef drip-loss values and sarcomere length*

	Drip-loss (mg/100 g)	Sarcomere length (μm)
Mean ± s.d.	43.8 ± 9.47	2.02 ± 0.36
Breed-cross (Bc)	ns	ns
Production system (Ps)	0.042	ns
Implant (Imp)	ns	ns
β-agonist (βag)	0.017	ns
Suspension (Susp)	<0.001	<0.001
Ps × βag × Susp	0.012	ns
Individual	0.008	0.017

Only significant interactions ($P > 0.05$) are reported.
ns: $P < 0.05$.

Table 2 *Full model adjustment (R^2) and relative contribution (% within model) of individual factors to the final variation in beef drip-loss values and sarcomere length*

	Drip-loss (mg/100 g)	Sarcomere length (μm)
R^2	0.58	0.76
Breed-cross (Bc)	–	2.85
Production system (Ps)	15.3	4.91
Implant (Imp)	–	–
β-agonist (βag)	19.5	–
Suspension (Susp)	44.3	91.1
Individual	8.52	0.52

Only interactions explaining >5% for any trait are reported.

Proximate analysis

The effects of breed-cross, implant strategy and ageing time were significant ($P < 0.05$) for moisture, fat and protein content in both *longissimus* and *semimembranosus* muscles (Table 3). Moisture and fat content in *longissimus* muscle were also affected ($P < 0.05$) by the production system, whereas the use of β-agonists influenced ($P < 0.05$) the moisture content in *longissimus* and the protein content in *semimembranosus* muscles. Several two- and three-way interactions were also statistically significant ($P < 0.05$). Carcass suspension had no effect ($P > 0.05$) on meat composition. Thus, the model was able to explain a large proportion ($R^2 = 0.80$) of the variability for moisture and fat content, but a smaller proportion ($R^2 = 0.48$) of the variability in protein content in *longissimus* muscle (Table 4). For *semimembranosus* muscle, more than half ($R^2 = 0.50$ to 0.60) of the variability in meat composition was explained by the model. Breed-cross and implant were responsible for 45.1% and 58.2% of the variability explained by the model in moisture and fat content in *longissimus* muscle, respectively, whereas breed-cross, ageing time and the interaction between the production system and ageing time were, in general, the most influential factors for the composition of *semimembranosus* muscle.

Beef cattle breeds present different growth rates, resulting in different maturity levels and, therefore, different fat tissue development at similar ages (Mirzaei *et al*., 2011). Moreover,

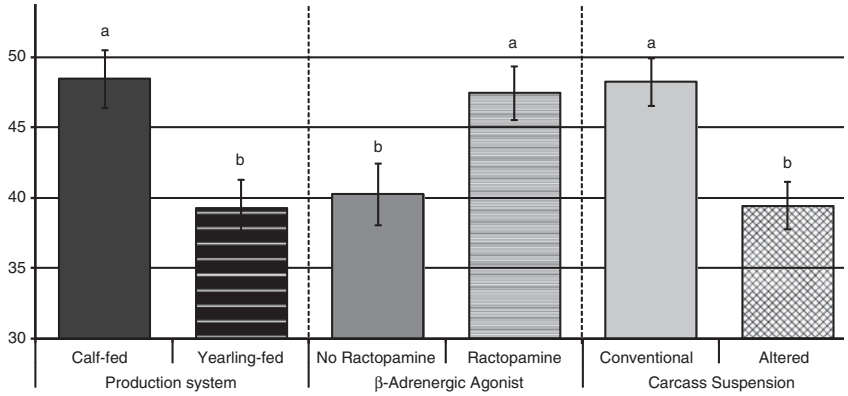

Figure 1 Effects of production system, β-adrenergic agonist and carcass suspension on beef drip-loss values. Different letters indicate statistical difference ($P \leqslant 0.05$).

Table 3 *Least square means (±s.d.) and factors (P-value) affecting beef (*longissimus *and* semimembranosus *muscles) proximate composition*

	Longissimus			*Semimembranosus*		
	Moisture (%)	Fat (%)	Protein (%)	Moisture (%)	Fat (%)	Protein (%)
Mean ± s.d.	72.0 ± 1.50	3.85 ± 1.82	23.1 ± 0.94	72.3 ± 1.45	2.51 ± 1.87	23.8 ± 0.97
Breed-cross (Bc)	0.014	0.001	<0.001	0.021	<0.001	<0.001
Production system (Ps)	0.031	0.024	ns	ns	ns	ns
Implant (Imp)	0.002	<0.001	0.030	0.021	0.008	0.041
β-agonist (βag)	0.028	ns	ns	ns	ns	0.015
Suspension (Susp)	ns	ns	ns	ns	ns	ns
Ageing (Age)	<0.001	0.022	0.001	<0.001	<0.001	0.004
Bc × Ps	0.002	0.017	ns	0.045	ns	ns
Bc × Imp	0.002	0.005	ns	ns	ns	ns
Bc × Age	ns	ns	ns	0.010	0.011	ns
Ps × βag	ns	ns	ns	0.015	<0.001	ns
Ps × Age	0.0391	ns	0.015	<0.001	<0.001	0.002
Imp × βag	ns	ns	ns	0.015	ns	ns
βag × Age	ns	ns	ns	ns	ns	<0.001
Bc × Ps × Age	ns	ns	ns	ns	0.001	ns
Ps × βag × Age	ns	0.043	ns	0.002	<0.001	0.012
Individual	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Only significant interactions ($P > 0.05$) are reported.
ns: $P < 0.05$.

the impact of implants on fat content has been widely discussed (Thompson *et al.*, 2008). Figure 2 shows the interaction between breed-cross and implant strategy for fat content. Interestingly, although no difference was observed when using implants on Continental beef cattle, the increase in fat content obtained with the increasing contribution of British breeds was reduced or eliminated by the use of hormonal implants. Therefore, although the decrease in fat content when implants are used in beef cattle is a well-known effect (Hunter, 2010), it may be breed dependant, resulting in greater changes in breeds with higher genetic potential for fat deposition. Intramuscular fat content has also been reported to increase with slaughter age and can be manipulated by dietary treatments (Ahnström *et al.*, 2009). Nevertheless, in this study the production system accounted for <1% of its variability. Finally, the loss in moisture over time during the ageing period (Juárez *et al.*, 2010) was likely responsible for the effect of ageing on meat composition.

Instrumental and sensory tenderness

Although extensive research has been developed during the last 20 years to understand the factors affecting beef tenderness, most studies only focus on a limited number of effects. This approach leads to small variability within the studies, whereas the variability observed under commercial conditions may be quite large (Butchers *et al.*, 1998; Ferguson *et al.*, 2001). Including numerous factors in order to increase this variability would lead to more applicable results. Moreover, to evaluate the contribution of the interactions among factors to the final variability, these need to be included in a single study. Thus, in this study, in which *ante-* and *post-mortem* factors potentially present in the commercial beef production chain

Table 4 *Full model adjustment (R^2) and relative contribution (% within model) of individual factors to the final variation in beef (*longissimus *and* semimembranosus *muscles) proximate composition*

	Longissimus			*Semimembranosus*		
	Moisture (%)	Fat (%)	Protein (%)	Moisture (%)	Fat (%)	Protein (%)
R^2	0.81	0.84	0.48	0.56	0.60	0.52
Breed-cross (Bc)	16.9	36.6	52.51	11.2	25.6	35.1
Production system (Ps)	–	0.5	–	–	–	3.02
Implant (Imp)	11.8	12.9	4.72	3.18	5.14	–
β-agonist (βag)	–	0.05	–	6.50	8.09	–
Suspension (Susp)	–	–	–	–	–	–
Ageing (Age)	13.6	2.07	3.64	11.9	4.23	3.11
Bc × Imp	16.4	8.73	–	1.88	1.43	0.00
Ps × Age	1.17	–	6.12	9.69	10.5	6.76
Bc × Ps × Age	–	0.05	–	7.81	4.46	0.60
Ps × βag × Age	1.55	2.92	–	8.51	11.4	9.16
Individual	21.37	23.09	11.80	26.2	17.6	33.9

Only interactions explaining >5% for any trait are reported.

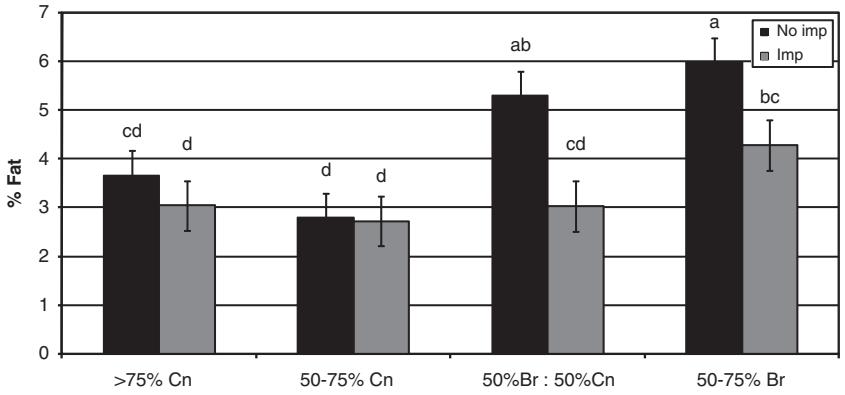

Figure 2 Effect of implant strategy on beef fat content (*longissimus* muscle). Different letters within factor indicate statistical difference ($P \leq 0.05$).

were included, the standard deviation observed for shear force in *longissimus* muscle was relatively large (2.02 kg). This large variability, similar to a commercial situation but under controlled conditions, allows a more accurate evaluation of the relative importance of each contributing factor, as well as their interactions.

The advantage of the approach used in this study that analyzes the relative contribution of the factors instead of multiple comparisons of means and their significance is evident when studying traits such as shear force. For the *longissimus* muscle, the effects of breed-cross, β-agonist strategy, carcass suspension and ageing time were significant ($P < 0.05$), but so were the effects of 20 two- and three-way interactions (Table 5). Interpreting these results might become an impossible task if the relative importance of each of these factors could not be estimated.

The data presented in Table 6 show how the suspension method and ageing time, as well as their interaction, explained ~70% of the variability in shear force explained by the model ($R^2 = 0.76$). Besides the individual animal variation (5.09%), no other factor explained >5% of the variability in shear force. Breed-cross, production system, β-agonist strategy, carcass suspension and ageing time affected ($P < 0.05$) shear force in *semimembranosus* muscle (Table 5). In this case, only a few interactions had an effect ($P < 0.05$) on shear force values. Looking at the relative contribution of these factors (Table 6), although the variance explained by the model was lower than for *longissimus* muscle ($R^2 = 0.55$), the suspension method and ageing time as well as their interaction absorbed ~45% of this variability. Other factors such as breed-cross, finishing treatment and their interaction explained ~20% of the variability. Suspension method, ageing time and their interaction were also the main factors influencing sensory initial and overall tenderness in both muscles. In *longissimus* muscle, these factors accounted for 70.7% and 65.9% of the variability in initial ($R^2 = 0.61$) and overall ($R^2 = 0.66$) tenderness, respectively, and 79.6% and 74.6%, respectively, in *semimembranosus* muscle ($R^2 = 0.49$ and 0.52, respectively).

On the other hand, a small proportion of the variability observed in initial juiciness was explained by the model ($R^2 = 0.26$ and 0.30 for *longissimus* and *semimembranosus*

Table 5 *Least square means (±s.d.) and factors (P-value) affecting beef (*longissimus *and* semimembranosus *muscles) shear force and sensory traits*

	Longissimus					*Semimembranosus*				
	Shear (kg)	IT	IJ	SJ	OT	Shear (kg)	IT	IJ	SJ	OT
Mean ± s.d.	5.56 ± 2.02	5.90 ± 1.45	5.67 ± 1.10	5.61 ± 1.51	6.22 ± 1.04	6.68 ± 1.40	4.92 ± 1.45	5.18 ± 1.16	5.08 ± 1.43	5.42 ± 1.14
Breed-cross (Bc)	0.022	<0.001	ns	ns	<0.001	0.016	0.032	0.027	0.002	ns
Production system (Ps)	ns	ns	ns	ns	ns	0.032	0.026	ns	0.006	0.003
Implant (Imp)	ns	ns	ns	ns	ns	ns	0.003	ns	ns	0.007
β-agonist (βag)	0.011	ns	ns	ns	ns	0.009	ns	ns	ns	ns
Suspension (Susp)	<0.001	<0.001	<0.001	0.025	<0.001	0.029	<0.001	<0.001	0.020	<0.001
Ageing (Age)	<0.001	<0.001	ns	ns	<0.001	<0.001	<0.001	ns	0.004	<0.001
Bc×Ps	<0.001	ns	ns	ns	ns	ns	ns	ns	ns	ns
Bc × Imp	ns	ns	ns	ns	ns	0.038	ns	ns	0.006	ns
Bc × βag	<0.001	ns	0.035	ns	ns	ns	ns	ns	ns	ns
Bc × Susp	<0.001	<0.001	0.015	0.041	<0.001	ns	ns	0.040	ns	ns
Bc × Age	<0.001	<0.001	ns	ns	<0.001	ns	ns	ns	0.004	ns
Ps × Susp	ns	<0.001	ns	ns	<0.001	ns	ns	ns	ns	ns
Ps × Imp	0.006	ns	ns	ns	ns	ns	ns	ns	ns	ns
Ps × βag	0.025	ns	ns	ns	ns	ns	ns	ns	ns	ns
Ps × Susp	0.002	ns	ns	ns	ns	ns	ns	ns	ns	ns
Ps × Age	<0.001	ns	ns	ns	ns	ns	ns	ns	<0.001	<0.001
Imp × βag	<0.001	0.011	ns	ns	0.016	ns	ns	ns	ns	ns
Imp × Age	ns	<0.001	0.005	ns	<0.001	ns	ns	ns	ns	ns
βag × Susp	<0.001	<0.001	0.022	ns	<0.001	ns	ns	ns	ns	ns
βag × Age	0.034	ns	0.018	ns	ns	ns	<0.001	ns	0.011	0.005
Susp × Age	<0.001	<0.001	0.001	0.009	<0.001	<0.001	<0.001	<0.001	ns	<0.001
Bc × Ps × Susp	ns	<0.001	0.012	ns	<0.001	ns	ns	ns	ns	ns
Bc × Ps × Age	ns	0.008	ns	ns	ns	ns	ns	ns	ns	ns
Bc × Ps × Susp	0.049	ns	ns	ns	ns	ns	ns	ns	ns	ns
Bc × Ps × Age	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Bc × Imp × Susp	0.006	ns	0.017	ns	<0.001	ns	ns	ns	ns	ns
Bc × Imp × Age	ns	0.013	ns	0.023	0.013	ns	ns	<0.001	<0.001	ns
Bc × βag × Susp	0.009	0.024	0.002	ns	<0.001	ns	ns	ns	ns	ns
Bc × βag × Age	ns	ns	<0.001	ns	0.015	ns	0.007	ns	ns	ns
Bc × Susp × Age	ns	0.030	ns	ns	ns	ns	0.007	ns	ns	0.001
Ps × Imp × βag	0.029	ns	ns	ns	ns	ns	ns	ns	ns	ns
Ps × Imp × Age	0.014	ns	ns	ns	ns	ns	ns	ns	ns	ns
Ps × βag × Age	<0.001	<0.001	ns	ns	<0.001	0.022	ns	<0.001	ns	0.011
Ps × Susp × Age	0.007	ns	ns	ns	ns	ns	<0.001	0.040	ns	<0.001
Imp × βag × Susp	ns	ns	ns	ns	0.008	ns	ns	ns	ns	ns
Imp × βag × Age	ns	0.006	ns	ns	<0.001	0.026	ns	ns	ns	ns
Imp × Susp × Age	ns	ns	ns	0.029	ns	ns	ns	ns	ns	ns
βag × Susp × Age	0.008	ns	ns	ns	ns	ns	0.013	ns	ns	ns
Individual	<0.001	0.011	0.242	0.340	0.007	0.012	0.066	0.069	<0.001	0.046

IT = initial tenderness; IJ = initial juiciness; SJ = sustained juiciness; OT = overall tenderness.
Only significant interactions ($P > 0.05$) are reported.
ns: $P < 0.05$.

muscles, respectively). Moreover, although the variability explained in sustained juiciness in *longissimus* muscle ($R^2 = 0.44$) was mainly due to breed-cross, implant and several interactions, production system accounted for almost 43% of the variability in sustained juiciness in *semimembranosus* muscle ($R^2 = 0.50$). Therefore, the factors included in this study were more effective in explaining the variability in texture than in juiciness in beef. This may be due to the large effect of other factors not included in the model, such as animal stress, carcass chilling regime or meat cookery have on beef juiciness (Juárez *et al*., 2012).

Ultimate meat tenderness is highly dependent on the degree of alteration and weakening of myofibrillar structures, resulting in an increase in tenderness in aged compared with unaged meat (Koohmaraie and Geesink, 2006). Moreover, several authors have reported changes in both instrumental and sensory texture of beef from pelvic suspended compared with Achilles-suspended carcasses (Eikelenboom *et al*., 1998; Aalhus *et al*., 1999; Ahnström *et al*., 2009). Therefore, as indicated by our results, the greatest variation in shear force values is due to *post-mortem* changes. According to previous studies, tenderness can be affected by breed, age and production system (Christensen *et al*., 2011). Implant strategies have also been reported to decrease tenderness in beef (Thompson *et al*., 2008). In this study, although some *ante-mortem* factors had an effect on beef texture, the total contribution of all of them was minimal compared with the effect of *post-mortem* factors. The individual animal variation was also relatively small compared

Table 6 *Full model adjustment (R^2) and relative contribution (% within model) of individual factors to the final variation in beef (*longissimus *and* semimembranosus *muscles) shear force and sensory traits*

	Longissimus					*Semimembranosus*				
	Shear (kg)	IT	IJ	SJ	OT	Shear (kg)	IT	IJ	SJ	OT
R^2	0.76	0.61	0.26	0.44	0.66	0.55	0.49	0.30	0.50	0.52
Breed-cross (Bc)	–	–	–	10.4	2.37	5.67	–	16.8	10.4	–
Production system (Ps)	–	–	–	–	–	6.66	–	3.68	42.8	2.91
Implant (Imp)	1.41	4.07	14.2	16.2	1.76	4.56	4.87	3.34	5.77	8.30
β-agonist (βag)	0.69	0.29	3.93	3.23	–	7.33	–	4.67	2.55	–
Suspension (Susp)	9.90	23.4	18.8	–	28.1	4.32	–	35.6	8.16	18.6
Ageing (Age)	55.8	15.9	–	5.22	11.7	33.1	–	–	7.40	–
Bc × Ps	3.01	–	–	–	–	8.25	–	–	0.32	–
Bc × Imp	–	–	11.8	1.81	–	–	0.54	–	1.62	–
Bc × βag	–	1.80	0.64	6.84	0.62	–	0.16	–	–	0.82
Bc × Susp	0.21	6.01	6.90	2.49	4.81	–	–	–	–	–
Ps × Age	4.66	–	8.78	2.99	0.57	–	–	0.12	–	–
Imp × Age	0.97	0.68	5.34	–	0.77	0.41		1.26	0.73	0.32
Susp × Age	5.08	31.4	13.8	13.2	26.1	7.32	79.6	10.1	2.43	56.0
Ps × βag × Age	1.46	1.88	1.01	3.74	1.38	3.95	0.12	5.59	2.21	2.34
Bc × Ps × Age	0.62	0.94	–	–	0.06	–	–	6.18	6.70	0.97
Bc × Imp × Age	0.47	–	–	17.8	0.22	–	1.56	–	–	0.26
Bc × βag × Age	–	–	6.73	2.73	1.31	–	–	–	–	1.13
Imp × βag × Age	–	–	–	–	0.39	5.27	–	–	–	–
βag × Susp × Age	0.04	0.46	–	0.97	–	6.10	5.99	–	–	2.18
Individual	5.09	0.81	0.12	0.05	0.78	4.37	0.24	0.44	0.34	0.29

IT = initial tenderness; IJ = initial juiciness; SJ = sustained juiciness; OT = overall tenderness.
Only interactions explaining >5% for any trait are reported.

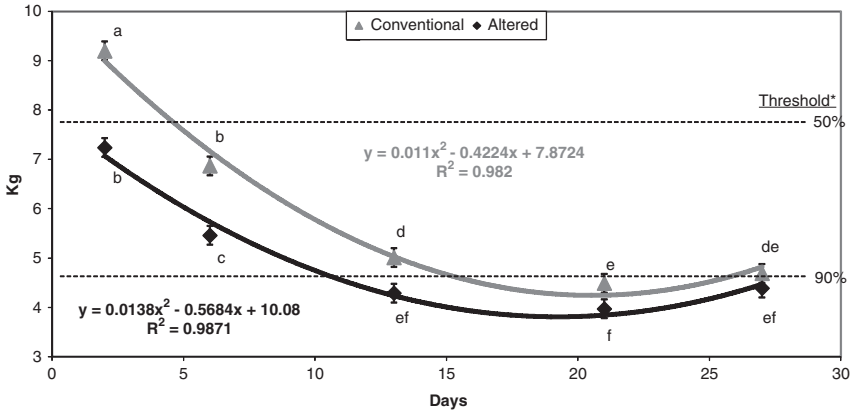

Figure 3 Interactive effect of carcass suspension and ageing time on beef shear force (*longissimus* muscle). Different letters indicate statistical difference ($P \leq 0.05$). *Percentage of consumers considering meat as tender at that shear force value according to Aalhus *et al.* (2004).

with other factors. In fact, the genetic variance in shear force for the type of breeds included in this study has been reported to be ~8% (Robinson *et al.*, 2001). However, as stated by Ferguson *et al.* (2001), the effect of the *post-mortem* conditions can negate any genetic advantage in tenderness an animal may have. Our results confirm that an appropriate *post-mortem* handling of the carcasses may be much more effective in controlling beef tenderness than *pre-mortem* strategies.

Due to the high relative importance of these factors, the interaction between carcass suspension and ageing time in *longissimus* muscle is presented in Figure 3. The large difference in shear force values (1.96 kg) between carcass suspension treatments observed at day 2 ($P < 0.001$) decreased over time until day 27 when shear force values were similar between both carcass sides ($P > 0.05$). Similar results, with decreases in shear force values >20% after using pelvic suspension, have been previously reported by several authors (Hostetler *et al.*, 1972). In this study, 50% of the steaks (*longissimus* muscle) from carcasses suspended by the aitch bone would be considered tender immediately after slaughter (0.05 day *post mortem*) according to the consumer thresholds for beef developed by Aalhus *et al.* (2004).

Steaks from conventional Achilles' tendon suspension would need to be aged for 4.39 days to obtain the same level of acceptability. In the same way, pelvic or aitch bone suspension would result in a 90% acceptability after 10.5 days of ageing, whereas conventional suspension would require 15.1 days of ageing to achieve similar results. Previous studies have shown how pelvic suspension reduces the need for longer ageing periods and significantly reduces the variation in tenderness (Ahnström *et al.*, 2009). *Rigor* sarcomere shortening is the cause of 24 h *post-mortem* toughening, and proteolysis is responsible for the decline in shear force during *post-mortem* storage (Wheeler and Koohmaraie, 1994).

The decrease in sarcomere shortening observed in carcasses suspended by the aitch bone resulted in smaller improvements due to proteolysis (Koohmaraie *et al.*, 1996). Moreover, the quadratic trend observed in both suspension treatments, showing a slight increase in shear force after extended ageing, has been previously reported and is related to increasing moisture losses over time and its interaction with cooking treatments (Juárez *et al.*, 2010). These two effects could explain the reduction in the differences in beef texture between conventional and altered carcass suspension.

Relative contributions excluding carcass suspension

Although pelvic suspension may be a relatively common practice in many countries, its implementation in Canada is still scarce. Therefore, in order to evaluate the relative contribution of the rest of the factors included in the study, the statistical analyses were repeated excluding the values of the right carcass sides (aitch bone suspension) and the effect of carcass suspension, as well as all its interactions. Thus, for traits such as drip-loss, the R^2 increased up to 0.96. However, >68% of this variability was linked to individual animal variation and ~24% to β-agonist strategy. On the other hand, a small proportion of the variability in sarcomere length ($R^2 = 0.27$) was explained by the model, from which 35.0% was due to differences among breed-crosses and 55.6% to differences between production system. Although ageing had the largest contribution (54.8%, 45.9% and 47.1%, respectively) on the explained variability in shear force ($R^2 = 0.79$) and initial ($R^2 = 0.64$) and overall ($R^2 = 0.68$) tenderness, the relative contribution of breed-cross increased compared with the full model (16.1%, 17.5% and 12.7%, respectively). Similar results were observed for *semimembranosus* muscle.

Numerous studies make evident the high variability in shear force values from different beef breeds (Monsón *et al.*, 2005; Pereira *et al.*, 2009; Christensen *et al.*, 2011). Differences in carcass fatness and cooling rate, collagen and lipid content, fiber type, sarcomere length or enzymatic activity may be responsible for differences observed among genotypes (Juárez *et al.*, 2012). However, even after excluding the effect of carcass suspension from the model, the relative contribution of any *ante-mortem* factor to the final variability in instrumental or sensory tenderness was always lower than that of the remaining *post-mortem* factor (e.g. ageing time).

Conclusions

Although numerous factors can potentially influence the final tenderness in beef, the relative importance of each of them may be very different. Among all the factors included in this study, *post-mortem* treatments (carcass suspension and ageing time) were responsible for the largest changes in instrumental and sensory tenderness values. Although the contribution of breed-cross was larger in a model without altered carcass suspension, ageing time remained as the most important factor influencing beef tenderness. Therefore, under the conditions simulated in this study, controlling or manipulating beef tenderness by carcass ageing and altered carcass suspension would be more effective in controlling beef tenderness than manipulating *in vivo* factors, such as implant or β-agonist strategies or production system. In this context, a correct ageing strategy would be the most important factor to control in a system aiming to guarantee tenderness. Moreover, if carcass suspension could be modified, this would be the second most important factor to take into consideration when trying to predict, manipulate or guarantee tenderness. If only traditional Achilles' tendon suspension could be used, the genotype understood as the breed-cross or percentage of Continental and British breeds, would gain importance as an influencing factor on tenderness, although always at a lower level than ageing time.

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